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Article Addendum

Private ultrasonic whispering in moths

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Sound-producing moths have evolved a range of mechanisms to emit loud conspicuous ultrasounds directed toward mates, competitors and predators. We recently discovered a novel mechanism of sound production, i.e., stridulation of specialized scales on the wing and thorax, in the Asian corn borer moth, *Ostrinia furnacalis*, the male of which produces ultrasonic courtship songs in close proximity to a female (<2 cm). The signal is very quiet, being exclusively adapted for private communication. A quiet signal is advantageous in that it prevents eavesdropping by competitors and/or predators. We argue that communication via quiet ultrasound, which has not been reported previously, is probably common in moths and other insects.

In summer, the chorus of insects is commonplace. In tympanate insects, such as crickets, katydids and cicadas, sound plays an important role in transmitting/receiving information about, for example, location and identity (sex and species).[1] For efficient communication over long distances, sound emitted by insects is, in general, fairly intense [>70 dB SPL (decibel sound pressure level) at a distance of 1 cm].[1,2] Accordingly, it is not surprising that most studies to date on acoustic communication in insects have focused on loud audible sounds.

Evolution of Ultrasonic Communication in Moths

The majority of moths have ultrasound-sensitive tympanal ears, which evolved, it is believed, to counteract predacious bats that emit ultrasonic echolocation calls during foraging.[3,4] The ears of moths within the same superfamily are morphologically similar and located on the same position of a body, e.g., the thorax in Noctuoidea or abdomen in Pyraloidea,[4,5] suggesting that they developed independently before the divergence of superfamilies. Some moth species also evolved organs that emit ultrasound for communication in sexual and other contexts (Fig. 1). In contrast to the ear, various types of sound-producing organs, which differ in origin, are found within the same superfamily, suggesting that these organs evolved after acquisition of the ear.[3-5] It is assumed that moths evolved ultrasonic sexual communication through secondary exploitation of the preexisting ultrasound-sensitive ears (sensory bias model of signal evolution).[3,5]

Moths that produce loud ultrasound have elaborate sound organs,[3] such as the tymbals, which are found on the tegula,[6] thorax[7] or abdomen,[8] and the file and scrapers, which are found on the wing, leg[9] or on the genitalia (Fig. 1).[10] In moths, three types of ultrasonic songs for sexual communication have been reported: (i) a calling song for mate attraction,[8-13] (ii) a courtship song for mate acceptance/recognition,[2,6,14-16] and (iii) a duet between sexes for the male's approach to the female after pheromonal orientation.[17,18] In addition to sexual communication, male moths of genus Hecatesia express territorial calls with wing castanets,[19,20] while arctiid moths of both gender emit jamming or alarm clicks from thoracic tymbals in response to echolocation calls of predacious bats.[21-23] Other moth species are known to produce ultrasounds with abdominal,[24] thoracic[25] or wing[12] tymbals, although the function of these sounds are unknown. The ultrasounds described above are, without exception, characterized by the rather high sound pressure levels, ranging from 60 to 125 dB SPL at a distance of 1 cm (Fig. 1).

Private Ultrasonic Communication in *Ostrinia furnacalis*

Recently, we found that males of the Asian corn borer moth, *Ostrinia furnacalis*, produce ultrasonic courtship songs of extremely low intensity (46 dB SPL at 1 cm) in close proximity to a female (<2 cm).[2,26] Electrophysiological recordings from the auditory neurons of a female revealed that only females within 3 cm of the singing male can hear the song (Fig. 2).[2] The male moths produced these sounds by rubbing specialized scales on their wings against scales on the thorax (Fig. 3).[2] Sound production via specialized scales on the body surface is a novel discovery among insects. Simple sound-producing scales on the body might have evolved more easily than other more elaborate cuticular sound-producing apparatuses, requiring major modifications of the integument.

Our behavioral experiments have clarified the mode of action of the male songs in *O. furnacalis*.[2] The male songs suppress escape behavior, or movement in general, of the female, thereby increasing the mating success of the courting male (Fig. 4). The female response to the male courtship song may be cognate to freezing

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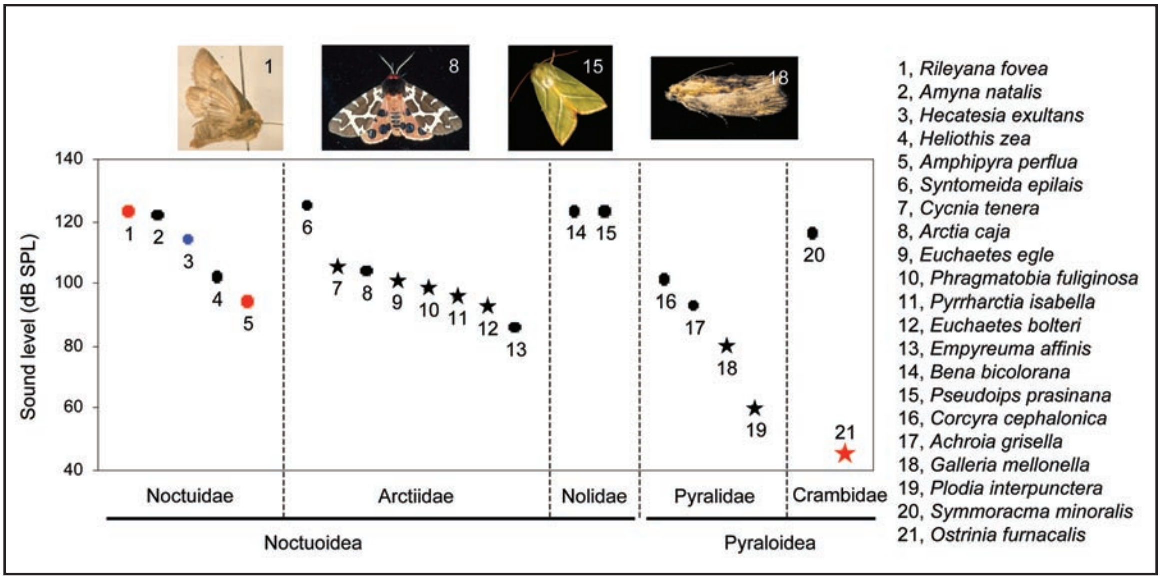

Figure 1. Ultrasound levels in sound-producing moths. Sound levels (0 dB SPL = 20 μPa) at a distance of 1 cm from the moths are shown for families within the noctuoid and pyraloid superfamilies.[2,8-10,12,14-16,18,20,23,25] Color of symbols indicates sound-producing mechanism: red, stridulation with file-scraper; black, click with tymbal; blue, percussion with alar castanet. A star indicates sound emission at a short distance. Top photographs show representative sound-producing moths. The sound level of the male song of *Ostrinia furnacalis* (red star) is the lowest among all sound-producing moths studied to date.[2]

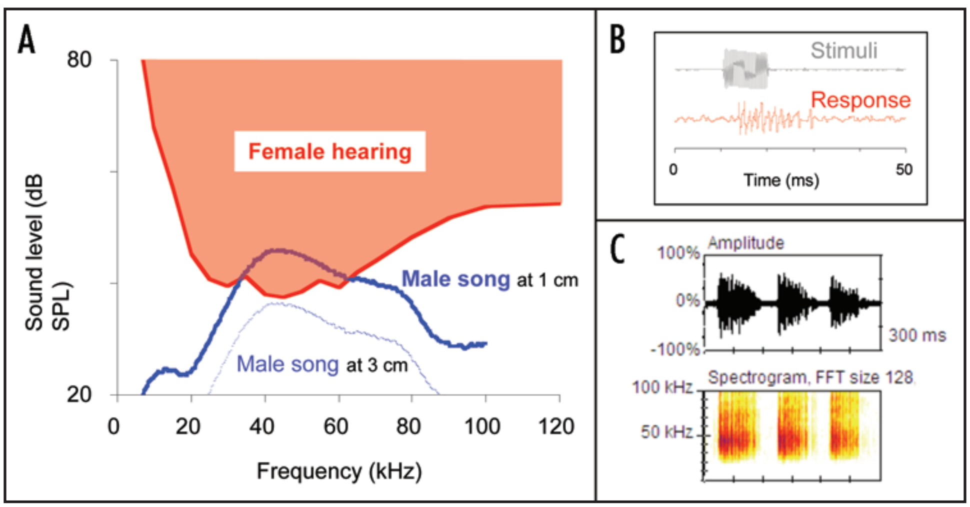

Figure 2. Male ultrasound and female audiogram in *Ostrinia furnacalis*. (A) Spectrum of the male ultrasound at a distance of 1 cm (blue solid line) shows main energy around 40 kHz, which corresponds to the most sensitive frequency range of female hearing (red line).[2] Male ultrasound at a distance of 3 cm (blue dotted line) is below the hearing threshold, indicating that the male song is not audible to females ≥3 cm distant. (B) Typical response of auditory neurons (red) to pulsed sine waves of 40 kHz (gray). (C) Oscillogram (upper) and power spectrogram (lower) of groups of ultrasonic pulses emitted by a male.

behavior, which is induced, as a defense maneuver, in response to the echolocation calls of insectivorous bats.[4] This raises the intriguing possibility that the moths have not only exploited the sensory apparatus, but also the behavioral reaction "inherited" from their interaction with bats. Thus ultrasonic communication in *O. furnacalis* should be an excellent system for testing the receiver bias model of signal evolution.[5,27]

Advantages of Whispering Communication

In insects, loud acoustic signals are often used for intraspecific communication over long distances. However, these signals are also susceptible to eavesdropping by unintended receivers (e.g., conspecific rivals, predators and/or parasitoids).[28,29] Indeed, communication via loud sounds is risky because predacious gleaning bats and parasitic tachinid flies, for example, locate sound-producing insects using passive hearing.[30,31]

The male courtship song of *O. furnacalis* has the lowest intensity (46 dB SPL at 1 cm) ever found in sound-producing moths (Fig. 1). What is surprising is that, within the animal world, such faint sounds can have a significant impact on mating. The utilization of quiet ultrasound is highly advantageous as it precludes eavesdropping by conspecific male competitors and natural enemies. Our discovery of extremely low intensity ultrasonic communication may reveal a world of private communication using quiet ultrasound.

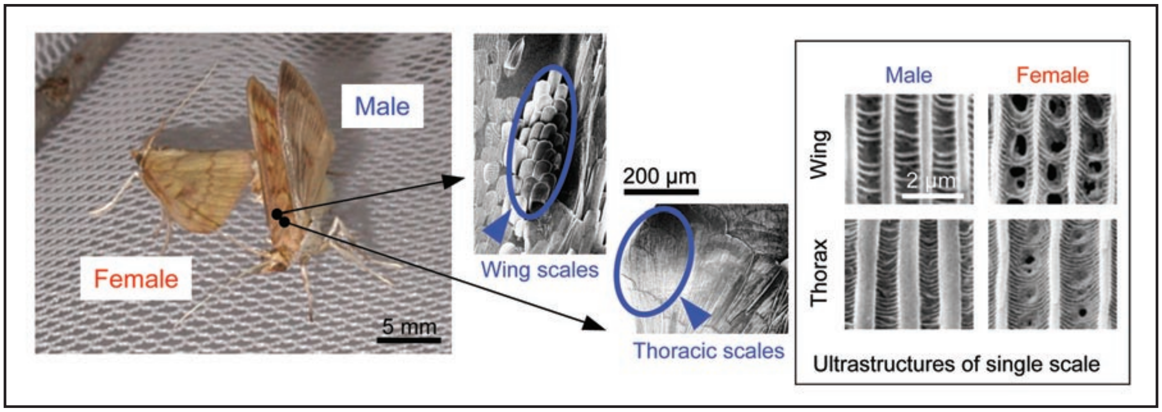

Figure 3. Sound-producing organ of male *Ostrinia furnacalis*. Courting male rubs specific scales on the base of forewings against scales on mesothoraces to emit ultrasonic song. Specialized sound-producing scales, which are characterized by thicker longitudinal ridges, are found only on the wing and thorax of the male (right box).[2]

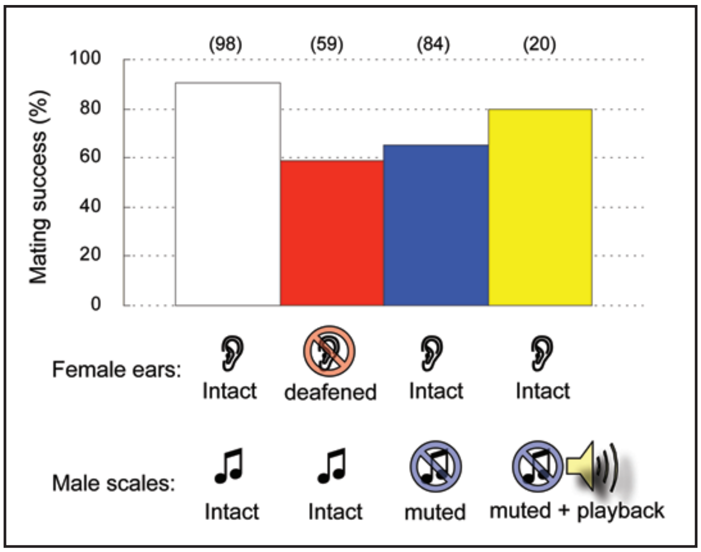

Figure 4. Effect of male ultrasound on mating success. Pairs of intact male and intact female showed high mating success (white bar). Mating success decreased when the female was deafened by puncturing the ear (red bar) or the male was muted by ablation of the sound scales (blue bar).[2,26] Playback of male song significantly compensated for the decrease in mating success in pairs involving muted males (yellow bar). Likelihood ratio test in generalized linear model, $F_{1, 2} = 19.5$, $p = 0.048$). Number of pairs examined is shown in parentheses above each bar.

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